Taxonomic and Bionomic Observations on a Floridian Panurgine Bee, *Perdita* (*Hexaperdita*) *graenicheri* Timberlake (Hymenoptera: Andrenidae)

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Abstract. — *Perdita* (*Hexaperdita*) *graenicheri* Timberlake is a solitary, gregarious, ground-nesting bee. It is more variable in color and male morphology than recognized previously. Males exhibit strong positive allometry in the relative size of a genal tubercle, in mandible length and width, and in length of the vertex. The species is believed to be univoltine with protracted emergence from late July to early November. Nest architecture and provisioning behavior are described, along with notes on immature stages. Relatively lengthy matings, 5-12 min., occur on flowers of *Heterotheca subaxillaris*, the pollen source. Information on plant hosts and associated insects is also provided.

Perdita is a monophyletic genus containing 769 named species and subspecies, ranging from southern Canada to Central America, with the apparent center of species diversity in the southwestern United States and northern Mexico (Hurd 1979, Ruz 1987, Rozen and McGinley 1988). These relatively small, panurgine bees are highly oligolectic (Linsley 1958).

Seventeen species of *Perdita* occur in Florida, six of which are restricted to the state, including *P. graenicheri* (Mitchell 1960). Many Floridian plants and animals reflect western affinities (Hubbell 1961), and the eastern *Perdita* are found primarily in sandy areas of the southern coastal plain (Mitchell 1960). Deyrup (1989) noted that many species of Florida arthropods have close relatives in the southwestern U.S., Mexico, and Central America. He suggested that this pattern provides evidence of an ancient continuous austral band of xeric habitat. The Florida peninsula today contains a series of inland sand ridges that functioned as biotic refuges during Miocene, Pliocene, and Pleistocene inundations (Neill 1957).

MATERIALS AND METHODS

Study Site.—Field work was done at the Archbold Biological Station, Highlands County, Florida, 8-14 August (BBN, KVK) and 28 December 1989 (BBN). *Perdita graenicheri* occurred at several of the terrestrial habitats at the Station, particularly in the sand pine scrub and southern ridge sandhill associations. Nesting data were obtained and many floral visits and matings were observed in the sand

pine scrub adjacent to the northeastern end of Lake Annie. Additional matings and floral visits were observed in the southern ridge sandhill area.

Bees nested in sunny, exposed patches having sparse vegetation (Fig. 1). Nesting substrate consisted of loose, small-grained, white quartz sand and particles of charred organic residue accumulated over years of scrub fires. All nests occurred in horizontal or slightly sloping areas where the sand was well drained, but moist just below the surface.

Voucher Material.— Specimens of *P. graenicheri* from this study are deposited in National Museum of Natural History, Smithsonian Institution (USNM), Archbold Biological Station, American Museum of Natural History, and Snow Entomological Museum (USNM). Specimens of the bee host plants, *Heterotheca subaxillaris* and *Chrysopsis microcephala*, are deposited in the U.S. National Herbarium (USNM).

Morphometrics.—Morphometric analysis of male head allometry was based on measurements of 41 specimens collected at the Archbold Biological Station in 1986 by M. Deyrup and in 1989 by KVK and BBN. Eight linear measurements (6 head and 2 thoracic, Fig. 2) were made with a binocular microscope equipped with an ocular micrometer. Means are given ± standard error of the mean (SEM).

Allometric relationships were calculated using reduced major axis regression of log-transformed data (Shea 1985, LaBarbera 1989). A multivariate estimate of overall size was first calculated for each specimen as the score on the first principal components axis, when the original eight variates were

Fig. 1. Sand road adjacent to Lake Annie, Archbold Biological Station. Bees nested in the exposed sand of roadside or in the center region between the wheel ruts.

analyzed by principal components analysis. The log-transformed linear measurements were then regressed on the log-transformed scores (overall size) to calculate scaling coefficients in the equation: $Y=bX^{\alpha}$. The null hypothesis of isometry is equal to an α of 1.0. The significance of the observed deviations of α from a slope of 1.0 were evaluated using a t-test (Sokal and Rohlf 1981).

Daily and Seasonal Activity.—Individual *Heterotheca* plants and *P. graenicheri* nests were monitored daily from ca 0800-1700 hrs, EST. Groups of composite flowers, or capitula, were observed for the presence of *P. graenicheri*, either as individuals or in copula, and for other insects. Nest entrances were covered with transparent plastic cups and were monitored for exiting or returning females in order to assess solitary/communal nesting behavior.

Bee specimens, collected on *Heterotheca* or in Malaise traps, from the Station collection were used to determine the seasonal occurrence of adults. Nests excavated in August and December also provided insights into the annual cycle of this species.

Nest Architecture.— Five nests were completely excavated from the surrounding substrate after blowing a fine mist of plaster of Paris powder into the entrances. Sand grains were removed with a teaspoon, pen-knife, or a #2 camel's hair paint brush. Additional substrate was removed from a 10 cm radius surrounding the main tunnel to locate plugged laterals.

Immature bees removed from excavated nests were either preserved in Kahle's solution for later dissection and description, or were placed in small wells in a covered plastic culture dish for laboratory rearing. Pollen balls still contained within open cells were carefully wrapped in tissue paper and transported in cork-stopped vials.

Immature Stages.— Living bee larvae were maintained in culture for as long as possible in covered plastic dishes containing moist paper towels, and were then preserved in Kahle's solution upon death. No adults were reared. Specimens were ultimately transferred to alcohol or freeze dried for examination by light or scanning electron microscopy.

Mating Behavior.—Foraging females and males were observed throughout the day (0800-1700 hrs, EST) on capitula of *Heterotheca* and *Chrysopsis*. Unimpeded matings were timed to the nearest second. Only matings viewed from initiation of contact until uncoupling, with no obvious outside interference, were recorded.

RESULTS

Taxonomy.— Until recently *P. graenicheri* Timberlake was known only from the short type series and a pair of topotypes collected by S. Graenicher in southern Florida (Timberlake 1947, 1956; Mitchell 1960). Five male paratypes (USNM) exhibited little variation in color pattern, and the genae were either unarmed or possessed only a very small tubercle (Fig. 2B). A series of 75 males and 90 females collected at the Archbold Biological Station by Mark Deyrup and ourselves shows more variation in male coloration and morphology.

In the males the pair of small, lateral face marks above the clypeus are occasionally lacking, and the pronotum may sometimes have a pair of small yellow markings. The differences in coloration are not related to the comparative size. Males are 3.5-5.0 mm long, and the forewings are 2.5-3.3 mm long.
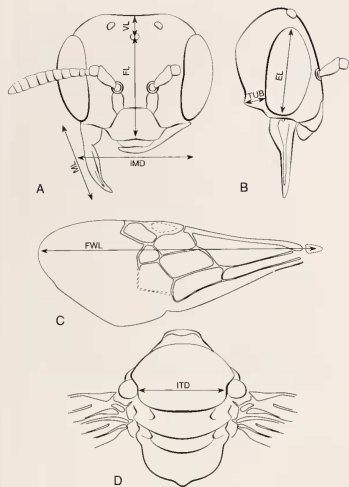
Fig. 2. A, Frontal view of head; B, lateral view of head; C, forewing; D, dorsal view of mesosoma. Eight linear measurements used in morphometric analysis are shown: VL = vertex length, FL = face length, IMD = intermandibular distance, ML = mandible length, EL = eye length, TUB = tubercle length, FWL = forewing length, ITD = intertegular distance.

Some females have the pair of transverse white markings on the fourth metasomal tergum reduced in size or lacking. The first tergum may be immaculate, but usually there is a pair of small lateral spots. Sometimes the first tergum may have an additional pair of small, central spots, and the four spots may be very narrowly separated from each other. Females are 4.5-5.2 mm long, and the forewings are 2.8-3.3 mm long.

Females key without difficulty to *P. graenicheri* in Timberlake's key to the subgenus *Hexaperdita* (1956). Larger males, however, may not key properly because the head is more subquadrate than rounded, and the gena has a large tubercle. There is no problem if one has an adequate series showing the allometric development of the head. But with a single large male, it may be necessary to extract the genitalia to separate it from *boltoniae* or *foveata*, to which it may key.

Neither sex keys properly in Mitchell (1960). Females will key to *graenicheri* (couplet 9) only if the markings on metasomal terga are changed from yellow to white. Only the smallest males, lacking both a tubercle on the gena and lateral face markings, key out at *graenicheri* (couplet 20). More small males would key out properly if the couplet were modified to indicate that lateral face markings usually are present though small. Males with a tubercle on the gena do not key correctly because Mitchell used presence or absence of a tubercle or spine in his first couplet to separate two groups of species, and *graenicheri* does not appear in the tuberculate group.

Morphometrics.— Table 1 presents the means and standard errors of the eight linear measurements. The regression analysis (Table 2) indicates significant deviation from isometry in six of the eight variables. The variables showing the strongest positive allometry are tubercle length (TUB), mandible length (ML), and vertex length (VL) (Fig. 3A,C,D). These trends reflect the fact that male head shape undergoes profound alterations with increased overall size (Fig. 4, A-F). Increased size results in disproportionate increase in tubercle length, mandible length, and expansion in the region of the head capsule dorsal to the median ocellus (vertex length, VL). Elongation of the tubercle is, in part, a result of an increase in overall genal width with increased body size. Tubercle length, with a scaling coefficient of 6.0, shows extremely pronounced positive allometry. A scaling coefficient of this magnitude indicates that a 20% increase in overall size results in a 3-fold increase in tubercle length. Other variables, such as eye length (EL), face length (FL), and forewing length (FWL) increase in proportion to overall size.

Daily and Seasonal Activity.— Bees were present on capitula on sunny days between 1000 and 1630 hrs. Males were present ca 30 min prior to females. During the peak foraging time, ca 1100 to 1430 hrs, several bees of both sexes were frequently encountered on a capitulum. Mating was observed throughout the foraging period. Both males and females remained active during periods of strong breezes, heavy cloud cover, and light rain. Females were observed initiating new nests as late as 1630 hrs. All nests observed or excavated contained a single adult female (n = 25).

This species is seemingly univoltine with a protracted emergence period so that adults may be present for several months. Newly transformed, teneral adults still underground were collected

during August 1989 in addition to flying adults. No adults developed from larval bees brought to the lab, however bivoltinism cannot be totally ruled out. Specimens collected by Mark Deyrup in 1986 bear labels indicating adult activity during late July, September, October, and early November. Nests excavated during late December contained only diapausing prepupae.

Nest Entrances.— Nest entrance/exit holes were circular, ca 3 mm in diameter, and never in the center of the tumulus. Radial tumuli were formed of loose sand grains pushed from the nest during a female's nest excavation. Each nest had only a single entrance. Entrances were closed with sand grains when a female was inside and remained open while she was away. Infrequently, a nest remained open while the female was inside, but nests were always closed at night.

Emergence holes (lacking tumuli) were numerous throughout the site, while entrances were more

Table 1. Means and standard errors of linear measurements, in mm (n = 41). See Figure 2 for measurements (TUB = tubercle length; EL = eye length; ML = mandible length; VL = vertex length; FL = face length; IMD=intermandibular length; ITD = intertegular length; FWL = forewing length).

TUB	0.17 ± 0.01
EL	0.69 ± 0.01
ML	0.67 ± 0.02
VL	0.10 ± 0.002
FL	0.87 ± 0.01
IMD	0.77 ± 0.01
ITD	0.85 ± 0.01
FWL	2.89 ± 0.03

dispersed and loosely aggregated. One entrance studied had an arrangement of small twigs encircling the opening. Upon displacement of the twigs to a location ca 6 cm away, the returning female flew directly to the center of the twigs instead of to her nest. This action was repeated for ca 8 min
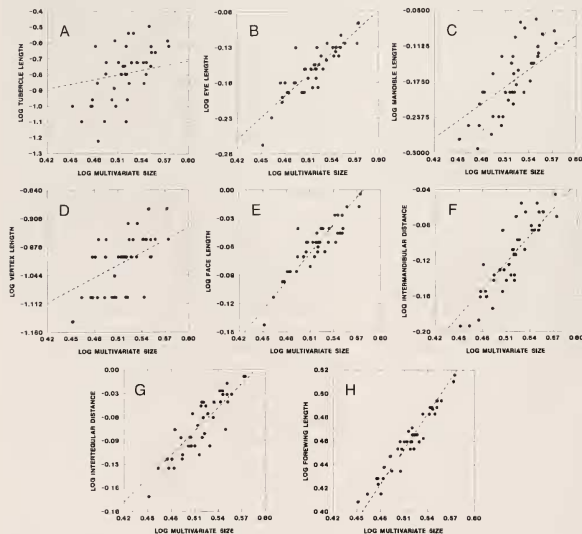

Fig. 3, A-H. Relationships between eight linear measurements and overall body size (data log-transformed) for 41 male *Perdita graenicheri*. Solid line indicates reduced major axis regression line and dashed line indicates null hypothesis of isometry (slope = 1.0). See Table 2 for major axis regression equations.

Table 2. Reduced major axis regression equations for eight linear measurements regressed on overall size. See Figure 2 for measurements (TUB = tubercle length; EL = eye length; ML = mandible length; VL = vertex length; FL = face length; IMD = intermandibular length; ITD = intertegular length; FWL = forewing length).

TUB = 1.26x10^{-4} (SIZE)$^{6.00}$	t = 6.65***
	s_a = 0.751
EL = 0.18 (SIZE)$^{1.14}$	t = 1.58 ns
	s_a = 0.089
ML = 0.058 (SIZE)$^{2.14}$	t = 5.14***
	s_a = 0.211
VL = 6.4x10^{-3} (SIZE)$^{2.28}$	t = 4.49***
	s_a = 0.286
FL = 0.29 (SIZE)$^{0.94}$	t = 1.02 ns
	s_a = 0.286
IMD = 0.15 (SIZE)$^{1.37}$	t = 3.68***
	s_a = 0.101
ITD = 0.18 (SIZE)$^{1.30}$	t = 3.05**
	s_a = 0.097
FWL = 0.98 (SIZE)$^{0.90}$	t = 2.68*
	s_a = 0.036

before the bee finally located her nest entrance.

Burrows.— Nests consisted of a primary unlined shaft ca 3 mm in diameter, and a series of shorter unlined lateral shafts each of which ended in a single cell. Initially main burrows descended at an angle of ca 15° for distances of 2 to 7 cm. Then the main burrows turned abruptly downward, descending vertically for 23 to 42.5 cm. Lateral shafts were perpendicular to the main shaft and branched off of it at depths of 22 to 34 cm. They radiated in various directions horizontally from the main shaft and were 2 to 5 cm in length.

Laterals containing completed cells were filled with sand. The main burrow of one excavated nest had been filled with sand from 7 to 14 cm in depth.

Cells.— Cells were formed at the ends of laterals by enlargement of the tunnels to a diameter of ca 3.5 mm. Cells were ca 4 mm in length and sloped slightly downward toward the rear. A single cell was constructed at the end of the open lateral, provisioned, supplied with an egg, and then closed before another lateral and cell were excavated. The youngest cells were those deepest in the ground. Nests contained two to six cells, but because nest-

ing had been initiated only recently it is likely that nests excavated later in the season would contain a greater number of cells.

Upon first observing cells, they appeared to consist of unlined, non-manipulated sand grains. A drop of water placed in a cell was retained for several seconds, then flowed through. But cells gently removed from the substrate retained their shape and appeared to have a shiny, oily coating on the sand grains. Microscopic examination (light and SEM) of cells revealed a thin layer of a viscous material resembling nectar that bound the sand grains weakly to one another (Fig. 5A,C,D). The material did not have a sweet taste, was soluble in water after several seconds, and had a low melting point. Cell closures were indistinguishable from the sand grains plugging the laterals. However, all sand grains surrounding the pollen ball appeared to be impregnated by the cell binding material.

Provisions.— Pollen balls were perfect spheres consisting only of pollen of *Heterotheca subaxillaris* and nectar of *H. subaxillaris* or *Chrysopsis microcephala*. They were 2-2.5 mm in diameter, firm, and moist throughout. Completed balls were positioned in the rear of the cell and completely encased by a thin, presumably glandular, transparent coating (Fig. 5A,B). Like cell linings, pollen ball coatings initially repelled water, but became soluble within minutes, and dissolved in it.

Collected pollen was initially applied dry to trochanters, femora, and tibiae of the hind legs. As additional pollen was accumulated, pollen moistened with nectar was placed on top creating especially large bulges over the hindtibiae. Pollen brought into cells was deposited in the center and was not formed into a ball until the total provision was present. This pollen mass was slightly moist, but of a drier consistency than that of completed provisions, suggesting that additional nectar may have been added during formation of the ball.

Within the cells, both newly deposited pollen masses and completed pollen balls exhibited a very strong cheesy odor. Pollen on the legs of returning females did not have this odor, and pollen balls allowed to dry completely did not retain it. The odor, however, was so strong within the nest that the presence of a cell could be smelled before it was excavated from the plugged lateral. In fact, several undetected laterals were located by sniffing the substrate adjacent to the main shaft. Rozen (1967) noted that fermentation odors were not known from other panurgine nests.
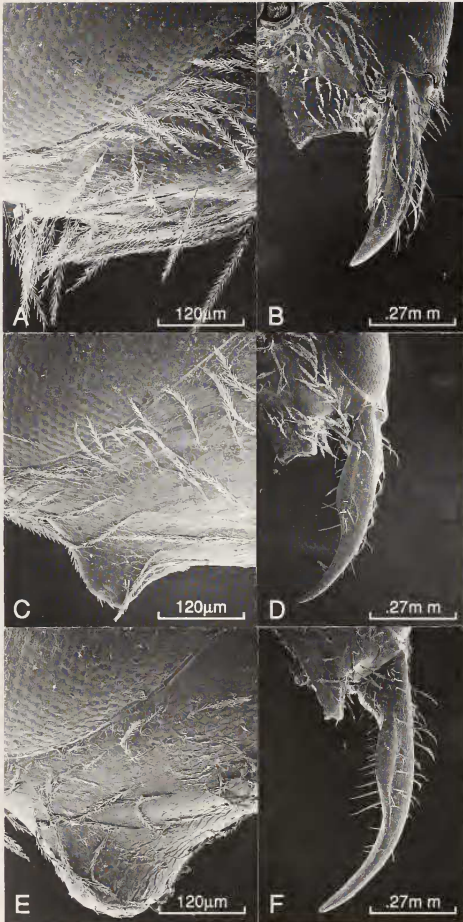
Fig. 4, A-F. Scanning electron micrographs of male *Perdita graenicheri* showing the left genal region (X250) and left mandible (X110). A and B show tubercle absent and short mandible. C and D show moderate tubercle and mandible. E and F show large tubercle and long mandible. Greater pubescence was noted for specimens lacking or with small tubercles.

Immature Stages.— Eggs were attached by their narrowed posterior ends to the top and rear of the pollen ball, farthest from the cell closure. Immature larvae were positioned upon their provisions while feeding, then rolled onto their dorsal surfaces prior to defecation. Prepupae rested in a curled U-shaped position on their large dorsal tubercles (Fig. 6A,B) with heads facing toward the cell closure. Fecal material consisted of a single string of pollen exines held on the venter until pupation, and remained with the exuvium. Quiescent, diapausing, post-defecating larvae demonstrated slow curling and uncurling movements. Indeed, wear to spines on the dorsal tubercles (Fig. 6C) was apparent in prepupae, but was not found in immature larvae. Cocoons were not present, but the prepupal integument was coated by a water-repelling secretion. This secretion (Fig. 6D) was relatively thick (ca 0.4 μ), unevenly distributed apparently due to several layers being secreted, and caused particles of debris to adhere to the larval cuticle.

Mating Behavior.— Males of *P. graenicheri* were never observed in or around nests. They were, however, numerous on and flying between the capitula of *Heterotheca* and *Chrysopsis*. Mating frequently occurred on the flower heads, while females gathered pollen. As noted for *P. texana* (Barrows et al. 1976), mating in *P. graenicheri* also was initiated prior to, during, or after all stages of pollen-nectar collection.

Males in most instances first landed next to females on capitula and then abruptly pounced on them. No apparent copulatory displays were observed, and males sometimes mounted pairs already in copula. Females were grasped from above, with the male initially holding her metasoma with his legs and her folded wings with his mandibles. Several seconds after initiating mating, however, males released their grasp, while remaining in copula, and either rested on the female's dorsum or at an angle of about 45 just above her. One female was observed actively grooming her metasoma throughout most of the copulation with apparent disregard of the male resting above.

Females of *P. graenicheri* seldom resisted copulation, but breezy conditions and the constant movement of swaying plants frequently resulted in foiled attempts to mate, as one or both bees were whisked away. We observed some females raising and lowering their metasomas as they walked across flower heads, which may indicate receptivity. Matings were of relatively long duration. Timed from initial union until an undisturbed separation occurred, they ranged from 5 min 27 s to 12 min 20 s (n = 10, mean = 7 min).

Patrolling males flew rapidly between capitula, following a horizontal, zigzag flight pattern when above flower heads, and then descending quickly in a zigzag pattern if a female was present. Two or three males frequently were present hovering over a capitulum and often landed to take nectar. Males displayed little aggression towards one another, other than occasional bumping. This bumping motion consisted of one male pushing his head, as he crawled or while in flight, into the metasoma of another male. Bumping was most often directed towards a copulating male. These apparent attempts to dislodge males in copula were seldom successful, and usually resulted in the mating pair moving to another part of the capitulum, beneath the flower head, or to an adjacent capitulum. One pair, observed during a union of 7 min 5 s, was bumped three times by two different males. At one point the male in copula reared back to almost 180°, but did not become disengaged, and quickly resumed his original orientation.

Pairs separated as abruptly as they had coupled with no obvious post-copulatory behavior. Following copulation, males either paused momentarily, and then flew to another capitulum, or obtained nectar for 4-10 s (n=25) before leaving the flower head. Females occasionally flew to adjacent flower heads, but more often resumed pollen or nectar collection on the same blossom. In contrast to the single matings reported for *P. opuntiae* (Bennett and Breed 1985), *P. graenicheri* demonstrated multiple matings. Two females were observed mating within 30 seconds of a previous mating on the same capitulum.

Plant Associations.— Both male and female *P. graenicheri* visited the abundant flowers of two species of golden aster. Pressed plant specimens were identified as *Heterotheca subaxillaris* (Lam.) Britton & Rusby and *Chrysopsis microcephala* (Small) Shinners. While both plants were common in the study site, *Perdita* were seen most frequently on *H. subaxillaris*. Mating pairs and pollen collecting were observed only on *Heterotheca*. *Chrysopsis* was visited for nectar, and the literature, while giving no pollen source, also records the bees as visiting flowers of *Chrysopsis tracyi* (Graenicher 1930). Major reviews (Rickett 1967, Radford et al. 1968, Long & Lakela 1971) indicate that species currently placed in *Chrysopsis* Ell., *Hererotheca* Cassini, and *Pityopsis* Nutt. should be included in a single genus, *Heterotheca*.
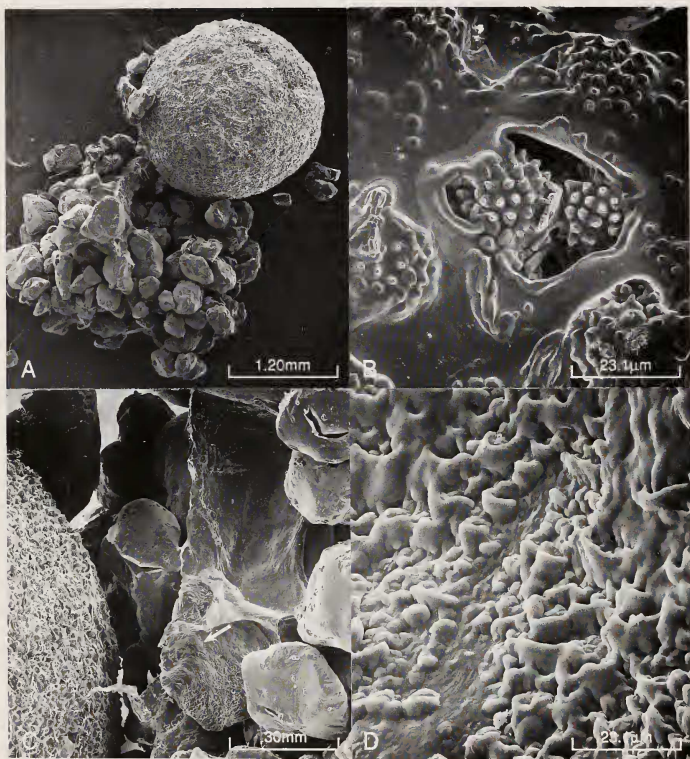
Fig. 5. Scanning electron micrographs from a *Perdita graenicheri* nest. A, Pollen ball showing water-repelling coating and several adherent sand grains (X25). B, Close-up of pollen ball showing *Heterotheca subaxillaris* pollen and a hole in the water-repelling coating (X1,030). C, Margin of pollen ball and adjoining sand grains with binding/water-repelling material (X100). D, Close-up of water-repelling material in sand grains (from region indicated in C.) (X1,030).

Associated Insects.— Two species of parasites, within the size range needed to enter *P. graenicheri* nests, were recorded at the nest site.

A female mutillid wasp, *Pseudomethoca torrida* Krombein, was collected near a number of *Perdita graenicheri* nest entrances. No other solitary bees were nesting in this circumscribed area, so it is possible that *torrida* is a parasitoid of this bee.

Danforth (1991b) found that *Pseudomethoca perditrix* Krombein parasitized post-defecating larvae of *Perdita portalis* Timberlake in New Mexico. This makes the association of *torrida* with *graenicheri* more probable. However, the closest relative of *torrida* is *frigida* (Smith), which is known only from halictine bee hosts.

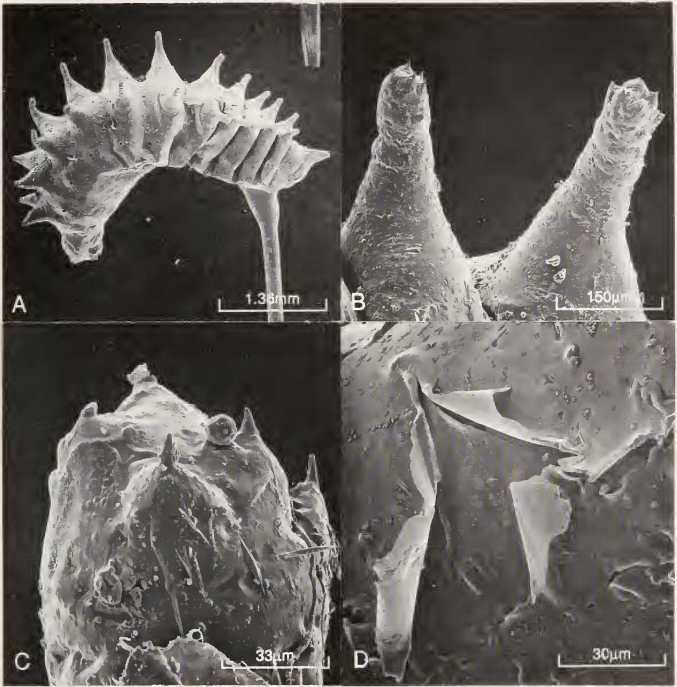Females of a small, cleptoparasitic halictid bee,

Fig. 6. Scanning electron micrographs of *Perdita graenicheri* prepupa. A, Entire prepupa showing large dorsal tubercles (X22). B, Tubercles are sclerotized and bear spines on their tips (X200). C, Close-up of tubercle showing debris adhering to the water-repelling secretion, and the wear to upper left spine (X900). D, Close-up of mid-region of a dorsal tubercle where the water-repelling secretion was cracked and peeling (X1,000).

Sphecodes sp., were noted inspecting nest entrances of *P. graenicheri* on two days, but none was captured. This species is a probable cleptoparasite of *P. graenicheri*.

Seven females and one male of a slender, delicate asilid fly, 3.0 to 3.5 mm long, were collected on the sand near nest entrances of *P. graenicheri*. They were not seen elsewhere on the surface of the sand, and were not observed entering bee nests. F.C. Thompson identified them as an undescribed species of *Townsendia* Williston. He believed that adults were not predaceous on the larger, rela-

tively stocky *P. graenicheri*, but suggested that their soil-dwelling larvae might prey upon the bee larvae.

Table 3 lists other species of Hymenoptera and Diptera collected on flowers of *Heterotheca* during the course of our study. All bees may be potential pollinators of *Heterotheca*, since each has a dense coating of pollen. Males of the bee-like *Tachytes distinctus* are also likely to be effective pollinators, since each has a dense coating of pollen on the thoracic sternum. The female bombyliids may also be capable of pollinating flowers of *Heterotheca*, since all of them had pollen grains on

Table 3. Species of Hymenoptera and Diptera collected on *Heterotheca* during the course of our study.

Hymenoptera
  Tiphiidae:
    Myzinum c. carolinianum (Panzer) 2 females, 1 male
  Scoliidae:
    Campsomeris plumipes fossulana (Fabricius) 1 male
  Vespidae:
    Eumenes s. smithii Saussure, 1 male
    Pachodynerus erynnis (Lepeletier) 1 female, 1 male
  Larridae:
    Tachytes distinctus Smith 3 males
  Nyssonidae:
    Bicyrtes capnoptera (Handlirsch) 1 female, 1 male
  Halictidae:
    Augochloropsis metallica (Fabr.) 1 female
    Halictus ligatus Say 7 females, 1male
    Dialictus nymphalis (Smith) 1 male
    Dialictus tamiamensis Mitchell 1 female
    Dialictus tarponensis Mitchell 2 females
    Dialictus tegularis (Robertson) 1 female
  Megachilidae:
    Megachile (Acentron) albitarsis Cresson 1 female

Diptera
  Bombyliidae:
    Systoechus solitus (Walker) 1 female
    Geron senilis (Fabricius) 1 female, 10 males
    Systropus angulatus (Karsch) 1 female, 4 males
    Lepidophora lepidocera (Wiedemann) 1 male
    Exoprosopa species 1 male
  Syrphidae:
    Copestylum mexicanum (Macquart) 1 male

the proboscides and foretarsi (N. Evenhuis, pers. comm.).

DISCUSSION

Taxonomy.— The study of specimens collected on *Heterotheca* and *Chrysopsis* in USNM and in the Archbold Biological Station collection convinces us that a revision of *Hexaperdita* is needed. In addition to the variation in color pattern and male morphology of *P. graenicheri*, we noted a greater degree of color variation in *P. georgica* Timberlake than recognized hitherto. Some specimens of the latter species also will not key out correctly in either Timberlake (1956) or Mitchell (1960).

Morphometrics and Mating Behavior.— One of the more striking characteristics of *P. graenicheri* is the extreme variation in male head size and shape. While males show considerable head shape change with increased size, female heads scale essentially isometrically with respect to overall body size. Larger males of *P. graenicheri* have disproportion-

ately long genal projections, mandibles, mandibular gape, and an expanded vertex. Larger males, however, suffer a "cost" associated with these allometric changes: disproportionately small wings. Such allometric tradeoffs have been observed between structures associated with fighting and with flying in several other insect groups, and are commonly interpreted as the result of sexual selection (Eberhard 1982, Thornhill and Alcock 1983, Crespi 1988).

Male head allometry is widespread among *Perdita* species in the subgenera *Macrotera* Smith, *Macroteropsis* Cockerell, *Cockerellula* Strand, *Pseudomacrotera* Timberlake, *Hexaperdita*, and among species in *Perdita* sensu stricto (e.g., *P. koebelei* Timberlake, *P. dentata* Timberlake [Timberlake 1964]), as well as other panurgine genera, such as *Psaenythia* Gerstaecker and *Arhysosage* Brèthes. *Perdita (Macrotera) texana* (Cresson) shows positive allometry in mandibular length and gape, and vertex length. Positive allometry in vertex length is related to a disproportionate expansion of the mandibular adductor muscles, which insert on the dorsal surface of the head capsule, with increased overall size. Therefore, all variables showing positive allometry can be traced to the mandibles, which are used by males in fighting, and in grasping females at the initiation of copulation (Danforth and Neff in press). Positive head allometry appears to be a precursor of male dimorphism in *P. (Macroteropsis) portalis* Timberlake (Danforth 1991c) and *P. (Macroteropsis) mellea* Timberlake (Rozen 1972). The flightless, large-headed males in *P. portalis* also have genal projections, which appear to perform a defensive role, protecting the membranous proboscidial fossa and neck region from the mandibles of other males during fierce intranest battles that can end in the death of one combatant.

Head allometry in *P. graenicheri* may be related to mating behavior, but it is puzzling that *P. graenicheri* males show no obvious agonistic interactions on capitula. Males of other *Perdita* species with positive head allometry (e.g., *P. portalis* and *P. texana*), can typically be seen fighting while on flowers. Head size in *P. graenicheri* may function primarily in grasping females at the initiation of copulation, especially since females are, overall, larger than males and are quite capable of dislodging them. The 12 min 20 s (740 s) mating recorded for *P. graenicheri* is the lengthiest reported to date for any species of *Perdita*.

Nesting Biology.— This study presents the first detailed observations on the nesting biology of a member of the subgenus *Hexaperdita*. In terms of social behavior, *P. graenicheri* is similar to many species of *Perdita* sensu stricto, in which females nest solitarily. However, in a related species of *Hexaperdita*, *P. ignota* Cockerell, females nest communally, with up to 10 females per nest (n=6 nests excavated; Danforth 1991a). Communal nesting occurs in other *Perdita* subgenera (e.g., *Macrotera* Smith, *Macroteropsis* Ashmead, *Cockerellia* Ashmead), and this trait shows considerable inter- and intra-specific variation. For instance, *P. lingualis* Cockerell and *P. albipennis* Cresson, two closely related species of *Cockerellia*, differ in the number of females per nest; the former is communal with up to 20 females per nest, while the latter was found to be solitary (Michener 1963, Danforth 1989). The number of females sharing a nest may also vary intraspecifically, from females nesting singly to communal associations of more than 30 females per nest (Danforth 1989, Neff and Danforth 1992)

The nest architecture and provisions of *P. graenicheri* are, in general, similar to members of the *Perdita* subgenera *Perdita* and *Cockerellia*. As in *P. graenicheri*, members of these subgenera coat the pollen ball with a glandular secretion, while the cell walls are usually reported to lack a hydrophobic coating (Rozen 1967). The observation of a very weak, water-soluble cell coating in *P. graenicheri* raises the possibility that nectar is used to coat cells in other species. In contrast, species of the subgenera *Macrotera*, *Macroteropsis*, and *Macroterella* produce a glandular, hydrophobic cell lining but do not coat the pollen ball (Danforth 1991b, Neff and Danforth in press).

Perdita graenicheri makes uncharacteristically short lateral tunnels for *Perdita*. While laterals may extend away from the main tunnel for up to 10 cm in some species (e.g., *P. portalis*, Danforth 1991c), *P. (Perdita) luciae* Cockerell and *P. (Hexaperdita) ignota* are the only other *Perdita* known to construct cells in a tight cluster around the main tunnel (Danforth 1989, Danforth 1991a).

Immature stages.— Data on egg placement and larval feeding and development are similar to those for other *Perdita* species. Of note, however, is the wearing down of spines on the dorsal tubercles of prepupae. Rozen (1967) mentioned the role of dorsal tubercles in movement of panurgine larvae. Observations of *P. graenicheri* suggest that during larval movements the spines play a role in preventing abrasion of the cuticle by sand grains, and may

further assist in preventing fungal infections by keeping larvae out of direct contact with the substrate.

Plant associations.— *Hexaperdita* contains approximately 30 species that, like *P. graenicheri*, are oligolectic on various genera of Asteraceae, primarily the subfamily Asteroideae. Associations with composites is widespread in the monophyletic assemblage including *Hexaperdita* Timberlake, *Pentaperdita* Cockerell and Porter, *Cockerellia*, *Procockerellia* Timberlake, *Callomacrotera* Timberlake, *Allomacrotera* Timberlake, and the Octomaculata group of *Perdita* Smith, sensu stricto (Danforth 1991a).

Although *Chrysopsis microcephala* and *Heterotheca subaxillaris* are similar and perhaps congeneric (see above), foraging and mating behaviors of *P. graenicheri* indicated that the bees were recognizing two different plants. Inasmuch as *P. graenicheri* visits *C. microcephala* only for nectar, it would be interesting to discover whether other eastern *Heterotheca* would be visited and for what purpose. A comparison of *P. graenicheri* behaviors to those of western *Perdita* species that visit *Heterotheca* might also be revealing.

ACKNOWLEDGMENTS

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